

MORPHOLOGY AND FUNCTION OF EXOTHECAL PORE-STRUCTURES IN CYSTOIDS

by C. R. C. PAUL

ABSTRACT. Humatirhombs, humatipores, and diplopores have external respiratory exchange surfaces. Their thecal canals open internally and body fluids flowed through them in life. Four types of humatirhomb are distinguished on morphology and arrangement of canals. Raised and buried humatipores occur and diplopores may have had extensile podia in life.

All cystoid pore-structures were respiratory. Exothecal pore-structures were individually less efficient in exchange than endothecal (dichoporite) pore-structures. Their relative inefficiency is due to requirements of protection and is counteracted by their large number per theca. Cystoids with exothecal pore-structures attain great size. Less efficient pore-structures (humatirhombs, humatipores) have shorter stratigraphic ranges and become extinct before more efficient types (pectinirhombs, cryptorhombs, diplopores).

Recent echinoderms as a group lack a specialized circulatory system and utilize varied exchange surfaces as did cystoids. Efficient exchange surfaces must be thinner than 1-3 mm: cystoid exchange surfaces are 0.01-0.1 mm thick. Diplopores and humatipores may have been connected to an internal water vascular system but humatirhombs were not. Rhombifera probably had external radial water vessels but *Diploporita* lacked them. Some Rhombifera may have had both internal and external branches of the water vascular system. Classes Rhombifera and *Diploporita* are defined and cystoid classification is reviewed.

THE cystoids constitute a heterogeneous grouping of primitive echinoderms which range from the basal Ordovician just into the Upper Devonian. The vital organs of cystoids (and other primitive echinoderms) were completely enclosed within a rigid cup or theca which provided them with protection. At the same time the theca restricted communication with the ambient sea water from which both food and oxygen necessary for life were obtained. The purpose of this paper is to show that three major types of pore-structure which occur in cystoids evolved in response to the respiratory 'problems' created by the rigid theca. These pore-structures in cystoids, and by implication similar pore-structures in other primitive echinoderms, were effectively gills.

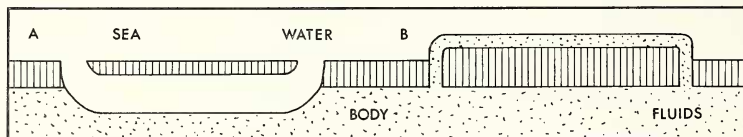
Traditionally cystoid pore-structures have been grouped into 'diplopores' and 'pore-rhombs' on morphological grounds. Functionally however division of all echinoderm pore-structures into endothecal and exothecal groups, where primary exchange from sea water to body fluids took place within and outside the theca respectively, is more appropriate (text-fig. 1). The morphology and function of endothecal (dichoporite) pore-structures in cystoids have been described (Paul 1968). The present paper considers exothecal pore-structures for which Hudson (1915, p. 166) originally proposed the term 'exospire'.

Three basic types of exothecal pore-structures occur in cystoids: one type of rhomb and two types of dipore. Brief descriptions of their morphology were given in Paul (1968). In the next two sections the morphology of exothecal pore-structures in cystoids is described and they are analysed functionally as exchange structures. Since the most likely form of exchange is oxygen and carbon dioxide transfer a section on respiration

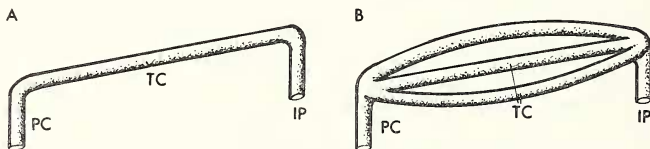
in recent echinoderms follows. The last two sections deal with the water vascular system in cystoids and with the taxonomic and evolutionary implications of this study.

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TEXT-FIG. 1. Diagrammatic representations of endothecal (A) and exothecal (B) canals. In A sea-water flows through the canal and exchange takes place within the theca; in B body fluids flow in the canal and exchange takes place outside the theca. Theca wall shown with vertical lines. In this and following diagrams the external medium is towards the top of the figure.



TEXT-FIG. 2. Simple (A) and compound (B) thecal canals. In A a single tangential canal (TC) connects a pair of perpendicular canals (PC); in B three tangential canals connect the perpendicular canals. Thecal canals open in internal pores (IP) in all exothecal pore-structures.

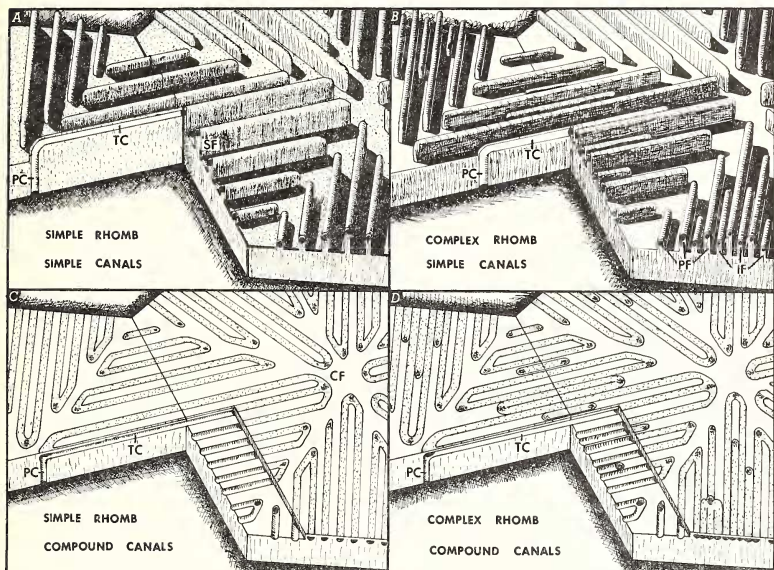
MORPHOLOGY OF EXOTHECAL PORE-STRUCTURES IN CYSTOIDS

All cystoid pore-structures are composed of U-shaped thecal canals (text-fig. 2) with one or more connections (tangential canals) between the limbs of the U (perpendicular canals). The openings (thecal pores) of exothecal canals are internal. The three types of exothecal pore-structures in cystoids are humatirhombs, humatipores, and diplopores s.s. (Paul 1968, p. 700).

1. *Humatirhombs* (text-figs. 3a-d, Pls. 1-4)

Humatirhombs (humare: Lat. to bury) are composed of a set of thecal canals (*fistulipores*, *fistula*, Lat. a canal), all of which arise from pores on the inner surface of one

plate, pass through the plate, and cross a plate suture to pores on the internal surface of an adjacent plate (text-fig. 3). The pores are always simple and circular (Pl. 4, fig. 2). The tangential canals may be single (simple fistulipores, text-fig. 3*a-b*) or multiple (compound fistulipores, text-fig. 3*c-d*) and they lie either just below the external sur-



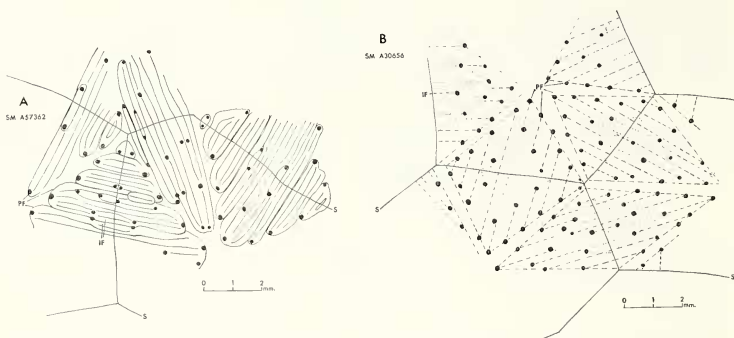
TEXT-FIG. 3. Four types of humatirhomb. A, simple humatirhombs with simple fistulipores (SF), B, complex humatirhombs with simple fistulipores, C, simple humatirhombs with compound fistulipores (CF), D, complex humatirhombs with compound fistulipores. In humatirhombs with simple fistulipores (A, B) the tangential canals (TC) are raised in ridges; humatirhombs with compound fistulipores (C, D) have tangential canals buried beneath plate surfaces. Complex humatirhombs (B, D) have both principal fistulipores (PF) and shorter intermediate fistulipores (IF). PC = perpendicular canal.

face (Pls. 3-4) or in the crests of ridges on the external surface of the theca (Pl. 1). Usually only simple fistulipores are associated with ridges (text-fig. 3*a-b*).

Four types of humatirhomb may be distinguished on the structure and arrangement of fistulipores. In *simple humatirhombs* all the fistulipores run the entire length of the rhomb from margin to margin (text-fig. 3*a, c*). *Complex humatirhombs* (text-fig. 3*b, d*) have additional shorter fistulipores within the intra-rhomb area. Both types of humatirhomb may be composed of either simple or compound fistulipores. Thus four types of humatirhomb may be recognized:

- Simple humatirhombs with simple fistulipores (text-fig. 3a)
 Complex humatirhombs with simple fistulipores (text-fig. 3b)
 Simple humatirhombs with compound fistulipores (text-fig. 3c)
 Complex humatirhombs with compound fistulipores (text-fig. 3d)

Humatirhombs are characteristic of, and confined to, the superfamily Caryocystitida, members of which have thecae composed of an indefinite and usually large number of thecal plates which are randomly arranged. The number of thecal plates often increases



TEXT-FIG. 4. Camera lucida drawings of the humatirhombs of *Caryocystites lagenalis* Regnéll to show principal (PF) and intermediate (IF) fistulipores. A, traces of tangential canals (SM A57362). B, traces of perpendicular canals (SM A30656) to show that intermediate fistulipores define smaller rhombs within the main rhomb. s = plate suture.

during growth and it is impossible to describe the position in a theca of an individual plate or rhomb. However since all plate sutures have rhombs developed across them and all rhombs of any one theca are invariably the same, distinction of individual rhombs is unnecessary. No part of a theca is better provided with rhombs than any other part.

EXPLANATION OF PLATE I

Stereophotos of simple humatirhombs with simple fistulipores.

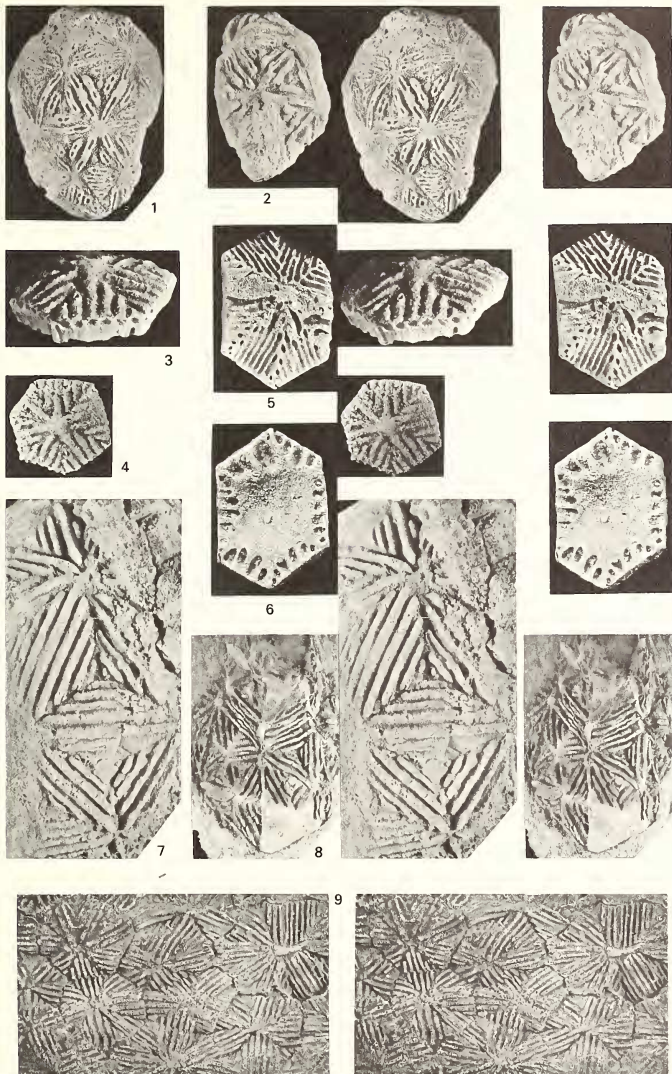
Figs. 1, 2, 7. *Lophocystis granatum* (Wahl.). 1, 2, Two small weathered examples to show fine granules on external surface. 1, RM Ec4353; 2, RM Ec4352; 7, SM A57330, Part of a large example with well-developed humatirhombs. All $\times 3$.

Figs. 3-6. *Ulrichocystis eximia* Bassler. 3, 4, Unweathered isolated plate; 3, oblique sutural view to show tangential canals beneath external ridges, $\times 6$; 4, external surface, $\times 4$. 5, 6, Another isolated plate; 5, weathered external surface to show exposed tangential canals and positions of perpendicular canals; 6, internal surface to show canals partially covered near plate centre, both $\times 4$ (cf. text-fig. 13b). Specimens in author's colln.

Fig. 8. *Lophocystis* sp. nov. (Shole'shook, S. Wales). SM A53070c. Latex impression of fragmentary example. $\times 2$.

Fig. 9. *Lophocystis malaisei* (Regnéll). SM A 50361. Latex impression of part of theca. $\times 2$.

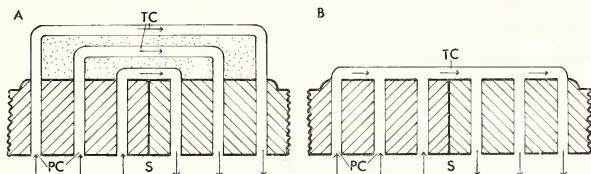
All figures whitened with ammonium chloride sublimate.



PAUL, Simple humatirhombs with simple fistulipores

The distribution of the four types of humatirhomb within the superfamily Caryocystitida does not correspond to taxonomic subdivisions. The first two types of humatirhomb (text-fig. 3a-b) are confined to the genera *Ulrichocystis* Bassler and *Lophotocystis* nov. (= *Heliocrinites* of the 'planata' group of Regnéll 1951, p. 22; Bather 1906, p. 18; see Appendix 2, p. 26). *Lophotocystis* has tangential canals developed in prominent ridges on the external surface of the theca (Pl. 1). The humatirhombs of *Ulrichocystis* are simple and their tangential canals are less distinctly raised (Pl. 1, figs. 3-4).

The third and most common type of humatirhomb (text-fig. 3c) occurs in all species of *Heliocrinites* s.s. (i.e. Regnéll's 'plicata' group, 1951, p. 22), all Echinospaeritidae and *Caryocystites dubia* (Angelin) = *C. angelini* Auctt. The fourth type (text-fig. 3d) occurs only in *C. lagenalis* Regnéll as far as is known.



TEXT-FIG. 5. Two possible interpretations of the structure of the canals in *Stichocystis* Jaekel as seen in longitudinal section. In A each pair of perpendicular canals (PC) is connected by a separate tangential canal (TC). In B a single tangential canal connects all perpendicular canals. The tangential canals were made entirely of soft tissue and are not preserved. Both the pairing of the perpendicular canals and the efficiency of currents (indicated by arrows) favour interpretation A. S = plate suture.

The genus *Stichocystis* Jaekel which on other morphological grounds belongs in the Caryocystitida bears unusual rhombs with sets of perpendicular canals developed in ridges on the external surface of the plates. Not all details of the structure of these rhombs are known but they seem to be functionally and morphologically related to humatirhombs. I interpret them as having a rhomb-in-rhomb structure (text-fig. 5a) but this is not certain. These rhombs may bear the same relationship to simple humatirhombs that multi-disjunct pectinirhombs bear to disjunct pectinirhombs.

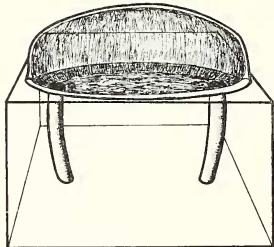
The next two types of exothecal pore-structures (diplopores and humatipores) are *dipores* which consist of a single thecal canal, not a set of canals (Paul 1968, p. 700).

2. Diplopores (text-figs. 6-8, Pls. 5-6)

Diplopores are dipores composed of a simple thecal canal, the tangential portion of which was not normally calcified and probably formed a papula or podium in life. As a result only the pair of perpendicular canals is preserved in fossils, which led Müller (1854) to propose the term 'Doppelporen' or diplopore (see Huxley 1854).

If a diplopore is considered as a functional rather than a morphological unit, the pores are internal and the supposed podium represents the tangential portion of the thecal canal (text-fig. 6). No podium has yet been found preserved but diplopore

tangential canals are sometimes calcified in the Aristocystitidae and Sphaeronitidae. Normal diplopores show as two pores which are usually paired within a shallow depression (*peripore*) on the external surface of the theca. Peripores may have rims, or peripheral or central tubercles (text-fig. 7*a-d*). In general morphology, diplopores strongly resemble the pore-pairs of echinoids.



TEXT-FIG. 6. Diagrammatic representation of the structure of a diplopore. The two perpendicular canals open into a depression, the peripore, over which a podium or papula extended in life.

Only the two perpendicular canals of a diplopore are preserved in most fossils. They may pass straight through the plates, follow sinuous courses, or unite with one or more other perpendicular canals (text-fig. 8). Previously it has been assumed that when two perpendicular canals unite to form a Y-shaped canal both branches fed the same diplopore (e.g. Chauvel 1941, figs. 39*c-e*, p. 100). However, in the only example where I have been able to trace the course of the two branches they fed separate diplopores (text-fig. 8*b*). Functionally this is a more efficient arrangement since it allows circulation. In *Codiacystis* Jaekel and *Sphaeronites* Hisinger large pits,

off which a number of perpendicular canals branch, occur on the internal surfaces of the plates. These pits could be centres of radiation for afferent and efferent canals but this is not certain. They show up as prominent tubercles on internal moulds (e.g. Barrande 1887, pl. 19, figs. 30, 32-33, 35-36).

Diplopores show wide variations in morphology but no clearly defined types exist. Diplopores of certain genera and families may have characteristic morphology however (e.g. *Haplosphaeronis*, Pl. 6, figs. 1-3; *Sphaeronites* s.s. Pl. 5, figs. 1-2). Diplopores occur in all superfamilies of the Diploporita. They are usually randomly distributed over a theca but may be more prolific on certain parts of the theca (or of individual thecal plates) than on other parts. In the Aristocystitidae certain areas of the theca may have sealed canals. Usually these areas were permanently in contact with something solid

EXPLANATION OF PLATE 2

Complex humatirhombs with simple fistulipores.

Fig. 2. *Lophocystis araneus* (Schlotheim), RM Ec5370. Note intermediate fistulipores in rhombs.

Fig. 7. *Lophocystis* sp. RM Ec25233a.

Simple humatirhombs with compound fistulipores.

Fig. 1. *Heliocrinites stellatus* Regnéll, RM Ec25985. Note compound fistulipores with pairs of tangential canals.

Fig. 3. *Echinospaerites aurantium aurantium* (Gyll.), SM A57365. Note fistulipores reach plate centres.

Fig. 5. *Echinospaerites aurantium suecicus* Jaekel, SM A57343. Note large area without fistulipores in centres of large plates.

Figs. 4, 6. *Heliocrinites ovalis* Angelin. Two examples with weathered surfaces revealing tangential canals in groups of two and three, 4, RM Ec3324; 6, RM Ec3327.

Figs. 1, 2, 4, 6, 7, $\times 3$, whitened with ammonium chloride sublimate; Figs. 3, 5, $\times 5$, photographed under water.



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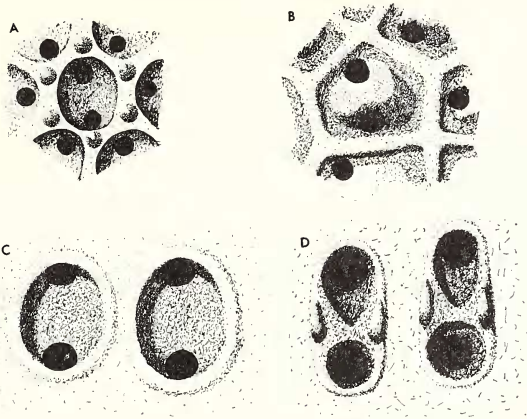


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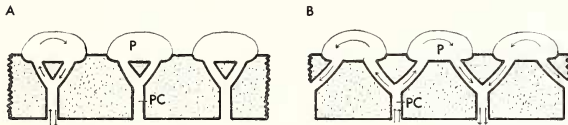


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PAUL, Complex humatirhombs with simple fistulipores



TEXT-FIG. 7. Four diplopores with different arrangements of tubercles and ridges associated with their peripores. A, *Sphaeronites pomum* (Gyll.). Oval peripores deeply impressed into the plate surface and with spine-like tubercles on the ridges between them (Pl. 5, fig. 2). B, *Sphaeronites globulus* (Ang.). Polygonal peripores with a large flat-topped central tubercle which produces moat-like channels within the peripore (Pl. 5, fig. 3). C, *Archeogocystis* sp. nov. (Shole'shook, S. Wales). Oval peripores with simple raised rims (cf. Pl. 6, fig. 4). D, *Haplophaeronis* sp. nov. (Shole'shook, S. Wales). Peripore divided into pyriiform and circular depressions by a subcentral ridge, peripheral ridge with two tubercles between pores (Pl. 6, fig. 2).



TEXT-FIG. 8. Two possible arrangements of Y-shaped perpendicular canals in diplopores. Current systems (indicated by arrows) are more efficient in B than in A. P = podia, PC = perpendicular canal.

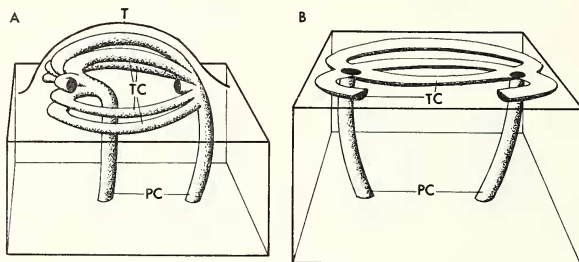
during life (e.g. ambulacral facets, attachment areas, etc.). In the Dactylocystidae diplopores are confined to five ambulacral tracts.

3. *Humatipores* (text-fig. 9, Pl. 7)

A *humatipore* is a dipore which consists of a wholly calcified compound thecal canal (text-fig. 9). In undamaged humatipores no pores show on the external surface. Two internal circular pores lead to two or more tangential canals which may lie either

beneath the flat external surface of the plates (buried humatipores, text-fig. 9b, Pl. 7, figs. 1, 5-10), or in a prominent external tubercle (text-fig. 9a, Pl. 7, figs. 2-4).

Humatipores are characteristic of, and confined to, the family Holocystitidae Miller. Buried humatipores occur in all five genera of Holocystitidae but tubercular humatipores are confined to the genera *Holocystites* s.s. and *Pustulocystis* Paul. Humatipores are always evenly developed over a theca.



TEXT-FIG. 9. Diagrammatic representations of the morphology of A, raised, and B, buried humatipores. In both, part of one tangential canal (TC) is cut away for clarity. PC = perpendicular canal, T = tubercle.

4. Haplopores

A number of species of the Aristocystitidae have been claimed (Bather 1900; Chauvel 1941) to bear haplopores: a type of pore-structure which consists of a single perpendicular canal. Since I have not examined all the relevant species I cannot state that haplopores do not occur in cystoids. However I have not seen a single specimen of a cystoid which characteristically bears haplopores and hence their functional morphology is not analysed. In the last fifty years or so Chauvel is the only person to have

EXPLANATION OF PLATE 3

Simple humatirhombs with compound fistulipores.

Figs. 1, 7. *Heliocrinites* sp. nov. (Rhiwlas, N. Wales). 1, GSM 102326, Part of an unweathered theca with tangential canals filled with dark sediment, $\times 5$, photographed under water. 7, GSM 102325, Stereophotos of weathered theca to show tangential canals in groups of two to four, $\times 3$.

Fig. 3. *Echinosphaerites aurantium americanum* Bassler. Example with tangential canals reaching plate centres (cf. Pl. 4, fig. 1), $\times 4$ (author's colln.).

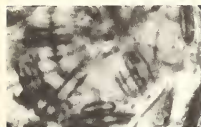
Figs. 4, 6. *Caryocystites dubia* (Angelin). 4, SM A57333, A large weathered theca. 6, SM A57335, Stereophotos of a small example to show tangential canals in groups of two to four, both $\times 2$.

Fig. 5. *Heliocrinites guttaeformis* Regnéll. RM Ec4780. An example with prominent tangential canals, $\times 3$.

Complex humatirhombs with compound fistulipores.

Fig. 2. *Caryocystites lagenalis* Regnéll. SM A57362. Stereophotos to show details of rhombs (cf. Pl. 4 fig. 6), $\times 6$.

All figs. except fig. 1 whitened with ammonium chloride sublimate.



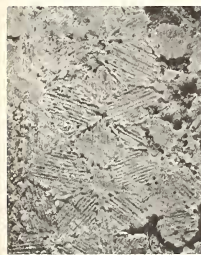
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PAUL, Simple humatirhombs with compound fistulipores

examined cystoid species which may bear haplopores. He wrote (1941, p. 60): 'If one reserves the name haplopores (canaux haploporiques) for these sinuous ramifying canals, the canals of *Aristocystis* [sic], *even though united in pairs*, are incontestably haplopores' (my italics). But if the perpendicular canals were paired circulation was possible and whatever modifications occurred within the plates, *functionally* the structure is the same as a typical diplopore (text-fig. 6). Hence I regard the pore-structures of *Aristocystites* as diplopores. Only one true haplopore has come to my notice in an isolated plate of *Eucystis* sp. from Knock, Westmorland which also bears several typical diplopores. I interpret this as a damaged or incompletely developed diplopore.

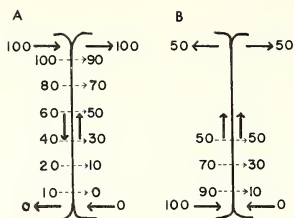
FUNCTION OF EXOTHECAL PORE-STRUCTURES IN CYSTOIDS

Unstable functional interpretations are inherently weak, since they can be neither substantiated nor disproved, and undesirable since they cast doubt on the validity of all functional interpretations. Many functional hypotheses are open to test however, by Rudwick's paradigm method (Rudwick 1964). To test a functional hypothesis the detailed morphology of a fossil structure is compared with that of an ideal structure (paradigm) which would serve the supposed function with maximum efficiency. Close comparison indicates that the fossil structure could have served the supposed function efficiently but does not prove that in fact it did so.

The paradigm method can be used to test the mechanics, but not the physiology of the structures investigated. It depends on acceptance of 'mechanical uniformity' (i.e. that the 'laws' of mechanics applied in the past as they do now) but may be totally independent of knowledge of living organisms. All morphological structures have more or less well-defined mechanical effects. Their function is taken to be that effect which is most beneficial to the vital needs of the organism or which confers most selective advantage on the organism. By considering effects rather than function, analysis may be made more rigorous and conclusions stated more positively. For example rigidity is an undeniable mechanical property of triangles. The triangulation 'ornament' of ridges connecting plate centres which is so commonly found in echinoderms undoubtedly increased the strength and rigidity of the test. This is not an interpretation: it is a fact. If we try to explain this effect in terms of function or selective advantage, then we make interpretations. In doing so we may draw sound conclusions if we can demonstrate that a vital function necessary for the survival of the organism (e.g. nutrition, protection, respiration, excretion, etc.) was performed more efficiently with, than without, the structure involved. Echinoderm tests with triangulation 'ornament' provided better protection for the enclosed vital organs than those without this 'ornament', by virtue of their increased strength and rigidity. Thus we may conclude that *most probably* the function of triangulation 'ornament' was protection but *undoubtedly* its effect was to increase the strength and rigidity of the test.

The following analysis is an attempt to estimate the mechanical efficiency of cystoid pore-structures as exchange systems and they are compared with the appropriate paradigm. Any exchange system must have an exchange surface to prevent mixing of fluids. The amount of exchange is controlled by the following factors:

1. The area of the exchange surface: the larger the area the greater the amount of exchange.
2. The resistance to exchange of the exchange surface: the thinner the surface the less its resistance will be.
3. The concentration gradient across the exchange surface: the higher the gradient (i.e. the greater the difference in concentration of the exchange substance on either side of the exchange surface) the greater the potential exchange. A counter-current system (text-fig. 10a) is the most efficient method of maintaining a high concentration gradient.



TEXT-FIG. 10. Idealized exchange systems. A, counter current; B, concurrent. Maximum potential exchange in B is half that of A. Figures represent percent concentration of the exchange substance. Heavy arrows indicate current directions, light arrows indicate exchange.

Thus the paradigm of an exchange system will have a large area of exchange surface which is as thin as is compatible with its strength and a counter-current system. A more detailed account of the above is presented in Paul 1968, pp. 708-709.

Detailed functional analysis

In exothecal pore-structures the fluids within the canals were body fluids. A healthy animal presumably had control over both their composition and circulation. Hence devices to prevent recirculation and choking of the canals by foreign particles were unnecessary and cannot in fact be recognized. The exchange surfaces were outside the theca and therefore liable to mechanical damage.

This brings into opposition two requirements of the paradigm: the thinner the exchange surface the greater the amount of exchange but the greater the chances of rupture and mixing. With the above ideas in mind the detailed morphology of exothecal pore-structures in cystoids will be compared with the paradigm of an exchange system and estimates of the efficiencies of the various types made.

1. *The area of the exchange surface.* Four of the five basic types of cystoid pore-structures have calcified exchange surfaces which are frequently preserved in fossils and the areas of which can be measured or at least estimated fairly accurately. Echinoderm skeletal material is a meshwork of fine calcite rods and soft tissue fibres; exchange would have taken place through the latter. Only about half the exchange surface area (the soft tissue half) functioned actively in exchange during life.

In cystoids individual calcified exothecal pore-structures are much less efficient than endothecal (dichoporite) pore-structures in terms of the area of exchange surface. The

EXPLANATION OF PLATE 4

Stereophotos of simple humatirhombs with compound fistulipores.

Fig. 1. *Echinospaerites aurantium americanum* Bassler. Weathered example with fistulipores which do not reach plate centres in largest plates, $\times 4$ (author's colln.).

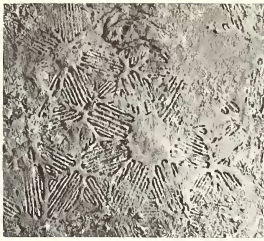
Figs. 2, 3. *Echinospaerites aurantium* s.l. 2, BMNH E7803, Internal surface of part of theca to show openings of perpendicular canals (cf. Pl. 1, fig. 6), $\times 2, 3$, BMNH (unreg.), Weathered portion of theca, $\times 3$.

Fig. 4. *Heliocrinites guttaeformis* Regnéll. RM Ec4763. Portion of weathered theca with large rhombs, $\times 3$.

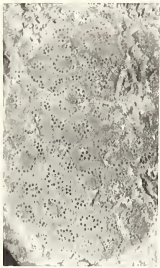
Fig. 5. *Caryocystites dubia* (Angelin). SM A57332. Example with unweathered external surface showing outlines of rhombs, $\times 2$.

Stereophotos of complex humatirhombs with compound fistulipores.

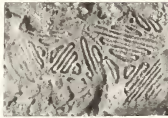
Fig. 6. *Caryocystites lagenalis* Regnéll. SM A57362. Note intermediate fistulipores, $\times 2$.



1



2



3



4



5



6



PAUL, Simple humatirhombs with compound fistulipores

ratio A_e/A_t where A_e is the area of the exchange surface and A_t is the area of the thecal surface occupied by the pore-structure is a measure of the efficiency of an individual pore-structure. In endothecal pore-structures this ratio is always greater than one and in one measured pectinirhomb was 7.84. Table 1 shows that this ratio varies from 0.28–0.86 in humatirhombs. All three types of exothecal pore-structure in cystoids exhibit modifications of their basic design which increase the ratio A_e/A_t but no evolutionary trends towards increased efficiency are apparent in contrast to pectinirhombs (Paul 1968).

TABLE 1. Estimates of the ratio A_e/A_t in humatirhombs

<i>Species</i>	<i>Ratio</i>	<i>Humatirhomb type</i>
<i>Lophocystis angustiporus</i> (Regnéll)	0.37	Simple rhombs with simple fistulipores
<i>L. granatum</i> (Wahl.)	0.30–0.42	" " "
<i>L. sp.</i> (Shole'shook)	0.28	" " "
<i>L. malaisei</i> (Regnéll)	0.28–0.41	" " "
<i>Ulrichocystis eximia</i> Bassler	0.59–0.67	" " "
<i>L. sp. nov.</i> (Skålberget)	0.42	Complex rhombs with simple fistulipores
<i>Heliocirinites ovalis</i> Ang.	0.58–0.68	Simple rhombs with compound fistulipores
<i>H. guttaeformis</i> Regnéll	0.38–0.80	" " "
<i>H. sp. nov.</i> (Rhiwlas)	0.43	" " "
<i>Echinospaerites aurantium</i> (Gyll)	0.29	" " "
<i>E. a. suecicus</i> Jaekel	0.75	" " "
<i>E. a. americanum</i> Bassler	0.57–0.77	" " "
<i>Caryocystites dubia</i> (Ang.)	0.71	" " "
<i>C. lagenalis</i> Regnéll	0.86	Complex rhombs with compound fistulipores

For simple fistulipores raised in ridges: $A_e \approx (1.5 \times FW)$, and $A_t = (RS + RW)$ where RS = ridge separation, RW = ridge width, and FW = fistulipore width.

For compound fistulipores buried in plates: $A_e \approx FW$ and $A_t \approx FW + IFW$. (IFW = separation of fistulipores.)

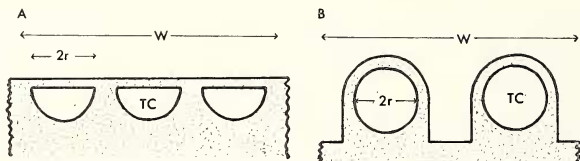
For complex rhombs the area covered by intermediate fistulipores is calculated and the ratio A_e/A_t doubled for that area, i.e. $\{A_e(\text{total}) + A_e(\text{complex})\}/A_t$. Thus if the complex rhomb area is half the total rhomb area the total exchange area = $1.5A_e/A_t$.

In an ideal simple humatirhomb without raised ridges the ratio of the width of the tangential canals to the width of the gap between them is a close approximation to A_e/A_t . When the two widths are equal A_e/A_t is approximately 0.5. Humatirhombs with compound fistulipores generally have more closely spaced tangential canals than those with simple fistulipores. However, the latter are usually raised in ridges and have a larger area of exchange surface than buried tangential canals (text-fig. 11). The increase in area due to the ridges is as much as 50%. Both arrangements (i.e. raised simple fistulipores and buried compound fistulipores) seem to be alternative methods of increasing the ratio A_e/A_t .

In terms of exchange surface area humatirhombs are individually much less efficient than dichoporite pore-structures. However, every plate suture bears a humatirhomb in all *Caryocystitida* and there are thus several hundred rhombs per theca. The total exchange area *per theca* was probably as high as in dichoporite cystoids with only 1–25 rhombs per theca. Since almost all the thecal surface is covered with humatirhombs the ratio A_e/A_t is only slightly greater than the ratio of the total exchange area to the total thecal surface area. Thus anything from about 25% to 75% of the thecal surface area

was exchange surface in humatirhomb-bearing cystoids but only about half actively functioned in exchange.

Humatipores are very similar to humatirhombs in terms of exchange area but it is much more difficult to measure or estimate A_e/A_t . An increase in the number of tangential canals increases the exchange area per humatipore (text-fig. 9*b*). Equally, raising the humatipore into a prominent tubercle increases exchange area (text-fig. 9*a*). With regard to exchange area *per humatipore* buried humatipores are less efficient than tubercular humatipores. However, the former are frequently more densely packed than the latter. Again this seems to reflect two alternatives: fewer, more efficient structures or a larger number of less efficient structures. In humatipore-bearing cystoids total



TEXT-FIG. 11. Diagram to illustrate the exchange areas of (A) buried, and (B) raised tangential canals (TC) in fistulipores. Width of exchange area in one canal in A is $2r$, in B it is πr . In rhomb width W and length l areas are $6rl$ in A and $2\pi rl$ in B. Since $\pi \approx 3$ two canals in B have the same exchange area as three canals in A.

exchange area *per theca* probably lies within the same limits as for humatirhomb-bearing cystoids.

Some diplopores resemble echinoid pore-pairs very strongly and probably gave rise to podia analogous, if not homologous, to echinoid tube-feet. The podia are never

EXPLANATION OF PLATE 5

Stereophotos of diplopores.

Fig. 1. *Sphaeronites* sp. nov. (Råbäck, Västergötland, Sweden). SM A35317. A small theca with densely packed diplopores over entire surface.

Fig. 2. *Sphaeronites pomum* (Gyll.) SM (unreg.). Note spinose tubercles between deeply sunken peripores (cf. text-fig. 6A).

Fig. 3. *Sphaeronites globulus* (Angelin). SM A57321. Note polygonal peripores with large flat-topped central tubercle (cf. text-fig. 6B).

Fig. 4. *Sphaeronites* sp. nov. (Skälberget, Dalarna, Sweden). SM A57407. Note irregular diplopores like those of *S. globulus*.

Fig. 5. *Sphaeronites pyriformis* (Forbes). BMNH E16340.

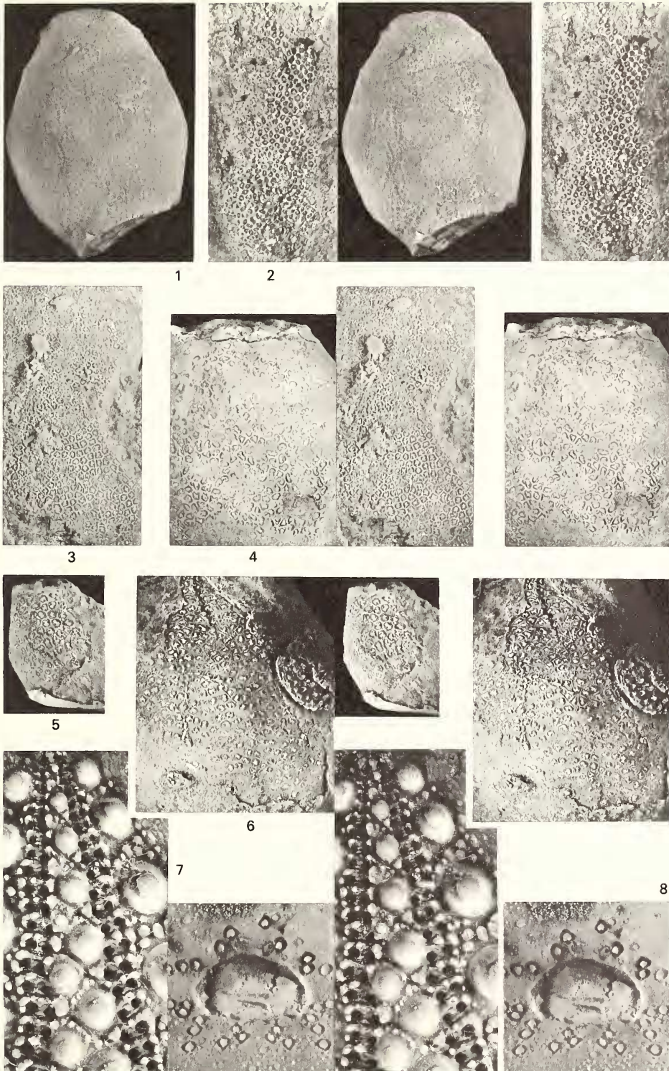
Fig. 6. *Sphaeronites lichii* (Forbes). GSM 7431. Note very prominent central tubercles (cf. fig. 8 this plate).

Stereophotos of echinoid pore-pairs.

Fig. 7. *Arbacia punctulata* (Lam.). Note tubercles around pore-pairs (author's colln.).

Fig. 8. *Echinocorys scutatus* (Leske). SM (unreg.). Pore-pairs of buccal tube-feet. Note large central tubercle (cf. fig. 6, this plate).

Figs. 1-6 $\times 3$, 7, 8 $\times 4$. All whitened with ammonium chloride sublimate.



PAUL, Diploporites

preserved, so measurement of their surface area is impossible. Nevertheless the area of podium wall could not have been less than the area of the peripore and since it was entirely made of soft tissue all the area could have functioned in exchange. Thus in diplopores A_e/A_i must have been greater than or equal to 1. Most diplopores have rims and tubercles associated with their peripores as do most echinoid pore-pairs. In the latter the rims and tubercles are attachment structures for the longitudinal muscles of the tube-feet (Nichols 1959, p. 70). As a broad generalization, the more strongly developed the rims, etc. are, the stronger the muscles and the greater the flexibility of the tube-feet. For example, many regular sea urchins have much more prominent rims and tubercles associated with pore-pairs on the oral surface up to the ambitus, and the tube-feet on this surface are the main ones used in locomotion. In some cases the comparison between diplopores and pore-pairs is so strong (e.g. *Sphaeronites* and *Echinocorys* oral tube-feet, Pl. 5, cf. figs. 3-6 with fig. 8) that the conclusion that they represent almost identical structures seems inescapable. Although impossible to prove, available evidence strongly suggests that some diplopores had extensile podia. This would increase their efficiency as exchange surfaces in two ways: it increases the area and it decreases the thickness of the exchange surface.

The density of packing of diplopores varies from genus to genus or even species to species. In *Archeocystis* the number of diplopores could apparently increase or decrease during life (Paul 1971). This forms a very delicate exchange mechanism that could respond to changes of the environment. Such was definitely not the case in *Sphaeronites*, all species of which have diplopores evenly developed all over the theca. The latter genus shows an interesting evolutionary trend towards larger diplopores throughout the Middle and Upper Ordovician.

Many representatives of the Aristocystitidae have sealed diplopores in some part of the theca. Chauvel (1966, p. 109) has interpreted this as a 'maladie calcaire' reminiscent of W. D. Lang's fatalistic trends in various calcium carbonate secreting organisms (Lang 1923a, b). Calcification of diplopores decreases their efficiency by at least halving their exchange surface area but it does not necessarily render them useless. Indeed calcification is much more likely to represent protection against predators eating soft tissue podia than ill health. Cystoids lacked spines, at least as far as is known; so podia were not mechanically protected as sea urchin tube-feet are.

The following conclusions can be drawn as regards area of exchange surface:

(i) Individual exothecal pore-structures are very much less efficient than individual endothecal pore-structures but far more of them are developed on any one cystoid. The total area for exchange *per theca* was probably the same for both endothecal and exothecal pore-structures. In humatirhombs available measurements indicate that the total exchange area was between 25% and 75% of the total thecal surface area.

(ii) In humatirhombs the raising of tangential canals in ridges, and the development of compound and additional fistulipores increase exchange area. In humatipores production of many tangential canals and development of tubercular humatipores both increase exchange area. Some diplopores may have had extensile podia which also increased exchange area. Within the limits of their geometry all three types of exothecal pore-structure tend to maximize their exchange area. Diplopores were probably the most efficient of the three but were liable to predation since their exchange surfaces were made entirely of soft tissue.

(iii) Although individually inefficient all exothecal pore-structures probably provided adequate exchange area per theca by sheer weight of numbers.

2. *The resistance to exchange of the exchange surface.* For maximum efficiency the exchange surface should be as thin as possible; however, rupture and mixing of fluids must be prevented. Exothecal pore-structures are much more susceptible to mechanical damage than endothecal pore-structures since their exchange surfaces are external. It is not surprising therefore that measurable exothecal exchange surfaces are thicker (0.05–0.10 mm) than endothecal exchange surfaces (always less than 0.03 mm and reaching as little as 0.007 mm). Nevertheless the thecal wall in most cystoids with exothecal pore-structures is 1–3 mm thick and often much thicker in aristocystitids. Chauvel (1966, p. 27) records a maximum thickness of 26 mm in *Maghreboecystis*. Although exchange surfaces of humatipores and humatirhombs are thicker than those of endothecal pore-structures they are still very much thinner than the thecal wall. Since no measurements of thickness are possible in diplopores their efficiency in terms of resistance to exchange cannot be estimated. However, extensible podia would have had very thin walls in all probability.

Exothecal pore-structures do not seriously weaken the theca and no strengthening structures have been recognized. Again this contrasts with pectinirhombs (Paul 1968).

3. *Maintenance of a concentration gradient.* The most efficient method of maintaining a concentration gradient is a counter-current system (text-fig. 10a). The best evidence for current directions is given by protective devices and devices to prevent recirculation. Unfortunately neither type of device is necessary with exothecal pore-structures since the fluids flowing in the thecal canals were body fluids. Neither type of device has been recognized. Some indirect evidence of currents and their directions of flow is available, however.

Nearly all recent echinoderms have ciliated external epithelia and cystoids probably had too. From purely hydrodynamic considerations fluids within the canals would not have moved without cilia due to the viscous effect of the boundary layer (Paul 1968, pp. 719, 721). Almost certainly both internal and external ciliary currents were present in cystoids. The humatirhombs of *Lophocystis granatum* (Wahlenberg) have fine granules developed on the ridges. In the best preserved example the granules are elongate parallel to the rhomb axes (Pl. 1, figs. 1–2). If a ciliated epithelium was present

EXPLANATION OF PLATE 6

Stereophotos of diplopores.

Figs. 1, 3. *Haplosphaeronis oblonga* (Angelin). 1, SM A57381, An example with oval peripores without rims. 3, SM A57356, An example with peripores with strongly raised rims.

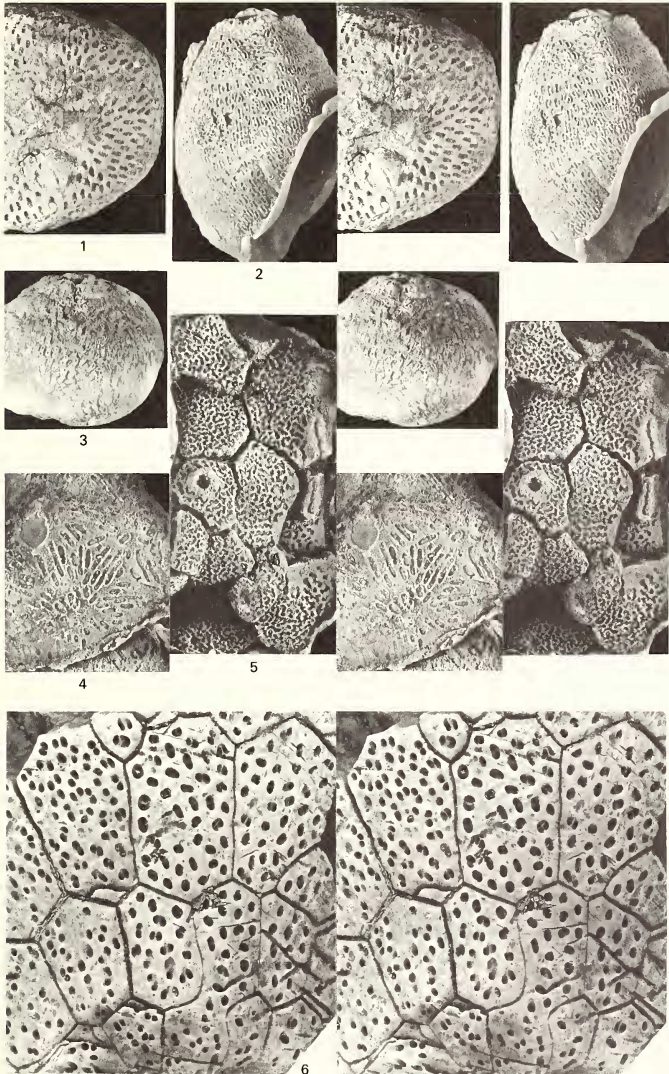
Fig. 2. *Haplosphaeronis* sp. nov. (Shole'shook, S. Wales). SM A57520. Latex impression of theca showing asymmetrical diplopores (cf. text-fig. 6d).

Fig. 4. *Arhegocystis stellulifera* (Salter). BMNH E16200. Latex impression showing elongate and oval diplopores with simple rims (cf. text-fig. 6c).

Fig. 5. *Aristocystites bohemicus* Barrande. SM A49868c. Latex impression showing irregular peripores between gonopore (left) and hydropore (right). Even though the peripores are very irregular it is still possible to see that the perpendicular canals are arranged in pairs as in typical diplopores.

Fig. 6. *Triamara* sp. USNM 166580. Example with small oval peripores. $\times 4$.

Figs. 1–5 $\times 3$. All whitened with ammonium chloride sublimate.



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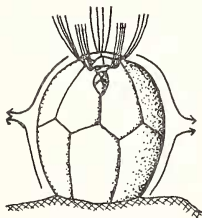
these granules would have increased the area of ciliated surface and enhanced the currents parallel to the rhomb axis. Such granules are similar to those on the periplastral areas of recent spatangoid sea urchins and are present on other species of *Lophocystis*. Granular ornament is also characteristic of most species of humatipore-bearing cystoids although the granules are not elongate. Since all the thecal surface is covered with humatirhombs in caryocystitid cystoids, external currents of different rhombs would interfere with each other. Nevertheless, water in contact with the external surface of the theca would be continually changed.

Evidence for the presence and direction of currents in *Diploporita* is virtually non-existent. However the genera *Holocystites* and *Haplosphaeronis* regularly have asymmetrical dipores and this asymmetry may be associated with current flow. Clearly, internal fluids came up one perpendicular canal and descended down the other. Which canal was efferent and which afferent is not certain in either genus. In *Holocystites*, which bears humatipores, one perpendicular canal is subcentral and one peripheral (text-fig. 9a, Pl. 7, figs. 2, 3). I suggest that body fluids ascended the subcentral perpendicular canal but the alternative direction seems equally plausible. From the point of view of exchange either direction would seem to be equally efficient.

Some species of *Haplosphaeronis* have asymmetrical diplopores. The peripore rim is thickened and raised and the peripore floor raised between the perpendicular canals, but closer to one than the other. Thus one canal opens in a roughly circular depression and the other in a pyriform depression (text-fig. 7d, Pl. 6, fig. 2). The diplopores of *Haplosphaeronis* are elongate and most are aligned in an oral-aboral direction. In the oral half of the theca the pyriform depression is adoral in the diplopore but the converse is true in the aboral half of the theca. If the theca was orientated with the mouth upwards, surface ciliary cleaning currents may have moved in an aboral direction on the upper half of the theca as they do in many recent sea urchins. A current in the reverse direction in the aboral half of the theca would also help to keep the theca clean (text-fig. 12). If such external currents were present, alignment of the diplopores parallel to them would allow internal counter-currents to operate. Recent sea urchins with specialized respiratory tube-feet have opposed external and internal currents. Again the opposite current directions would seem equally plausible and equally efficient in exchange.

The pattern of external currents proposed for *Haplosphaeronis* involves flow from the oral and aboral extremities towards the ambitus. Precisely similar current patterns were proposed for the external currents of dichoporite rhombiferans (Paul 1968). Since the two groups are not closely related, similar external cleaning currents may have preceded the evolution of internal respiratory currents. The latter probably developed in a fixed relationship to the former, namely counter to them.

In summary, there is little direct evidence for the presence or direction of currents in exothecal pore-structures. However, in at least one example of each major type there



TEXT-FIG. 12. Possible surface current directions in *Haplosphaeronis* Jaekel. Such currents would help to clean the thecal surface.

is some indirect evidence for currents. Indeed the basic morphology of thecal canals is ideal for current flow since one perpendicular canal could act as the afferent canal and the other as the efferent. In all but two genera the two perpendicular canals are identical and it is generally impossible to say which canal was which.

Conclusions

All three exothecal pore-structures (humatirhombs, humatipores, and diplopores) differ from the paradigm of an exchange system to some degree and they were individually less efficient than endothecal pore-structures in terms of the area and thickness of the exchange surface and possibly of current systems too. This relative inefficiency can be explained in terms of the need to prevent rupture of the exchange surface. Although individually less efficient than endothecal pore-structures, exothecal pore-structures still allowed exchange to take place. Indeed if currents were present this would inevitably have been their effect.

Large numbers of exothecal pore-structures are developed in any one theca which compensates for their individual inefficiency. For example, the ratio A_e/A_l is an estimate of individual efficiency in terms of exchange surface area. An average value for humatirhombs is probably about 0.5, for pectinirhombs about 10. In equal-sized thecae with equal-sized rhombs there should be 20 times as many humatirhombs as pectinirhombs to achieve the same amount of exchange. This ratio of humatirhombs to pectinirhombs is easily exceeded in practice since humatirhombs are developed in all available space on a theca. The exchange surfaces are thicker in humatirhombs than in pectinirhombs and hence the ratio should be higher than 20 to 1.

There can be little doubt that the mechanical effect of exothecal pore-structures in cystoids was to allow exchange between sea water and body fluids. Since oxygen and carbon dioxide transfer constitute the most likely form of this exchange, exothecal pore-structures were respiratory structures. It is now pertinent to consider respiration in more detail.

EXPLANATION OF PLATE 7

Humatipores.

Figs. 1, 5, 7. *Trematocystis globosus* (Miller). 1, USNM S3058b. Note tangential canals exposed by weathering. 5, 7, FMNH 8766a; 5, General view of plate, $\times 6$ approx. 7, Detail of humatipores to show plate meshwork in weathered tangential canals, $\times 25$ approx.

Figs. 2-3. Stereophotos of *Holocystites alternatus* (Hall). BMNH E7629. 2, Detail of single humatipore, $\times 25$ approx. 3, General view of plate showing tubercular humatipores with radiating tangential canals, $\times 6$ approx.

Fig. 4. *Holocystites scutellatus* Hall. Detail of some weathered tubercular humatipores, $\times 10$ (author's colln.).

Fig. 6. *Brightonicystis gregarius* Paul. SM A32814a. Detail of humatipores with 6-8 tangential canals, $\times 5$.

Fig. 8. Stereophotos of *Pentacystis sphaeroidalis* (Miller and Gurley). FMNH 6000. Detail of weathered humatipores, $\times 13$.

Fig. 9. Stereophotos of *Pentacystis simplex* Paul. AMNH 20271a. Detail of pit bored into cystoid by parasite which shows tangential canals of three humatipores parallel to the sides of the pit. These canals were formed after the pit was bored, $\times 10$.

Fig. 10. Stereophotos of *Trematocystis rotundus* (Miller).

All figures whitened with ammonium chloride sublimate.